

STUDIES IN THE *LEPIDAPLOA* COMPLEX
(VERNONIEAE: ASTERACEAE) V.
THE NEW GENUS *CHRYSOLAENA*

Harold Robinson

Abstract. — The genus *Chrysolaena* is described for seven neotropical species, most of which were previously placed in *Vernonia* series *Flexuosae*. The genus has the lophate and rhizomatous exine structure of *Lepidaploa*, but these xylopodial herbs differ in being mostly unbranched below the inflorescence, in having glanduliferous anther appendages, and in lacking basal nodes on the styles.

The present paper is the fifth in a series of seven devoted to the study of the neotropical *Lepidaploa* complex (Robinson 1987a, b, c) The group treated in the present study includes some well-known species of central and southern Brazil and adjacent Argentina and Bolivia. General similarity of habit and pubescence has resulted in some accurate grouping of the species in previous studies. Jones (1981) made the observation that all the species associated with the group had his type C pollen. The discovery of additional anther appendage and style base characters for the group during the present study has resulted in the recognition of the new genus *Chrysolaena*.

Previous treatments of species of *Chrysolaena* have recognized some of the relationships, but these treatments have always shown some omissions and have usually included some species that are not *Chrysolaena*. Both Baker (1873) and Cabrera (1944) placed the species that they recognized within the overall *Vernonia* Sect. *Lepidaploa*. Jones (1981) placed the group under sect. *Vernonia*, of which he made sect. *Lepidaploa* a synonym. In more detail, Baker (1873) placed the then known species now placed in *Chrysolaena* among others in his subsects. *Macrocephalae* and *Scorpioideae*. Two other species later considered to be related by Jones (1981), *V. simplex* and *V. deser-*

torum, were placed by Baker among other species in his subsect. *Oligocephalae*. Cabrera (1944) established subsect. *Flexuosae* for four species of Argentina, which all proved to be *Chrysolaena*; but like Baker, he kept *V. verbascifolia* separated in subsect. *Macrocephalae*. The recent study by Jones (1981) reduced the rank of the *Flexuosae* to a series. Jones included all the presently recognized members of *Chrysolaena* in his series, except the species commonly known as *V. hypochlora* (syn. *Chysocoma oligophylla*). He also included the two species of somewhat similar habit from Baker's (1873) subsect. *Oligocephalae*. Jones' (1981) description of series *Flexuosae* emphasized the xylopodial habit, the usual lack of branching below the inflorescence, the yellowish to brownish trichomes, the few to numerous sessile heads, the lanceolate acuminate to aristate involucrel bracts, the strigose to pilose achenes, and the type C lophate pollen. Only the two oligocephalous species violated the cited characters by having pedunculate heads.

The circumscription of the *Flexuosae* of Jones (1981) was believed to be totally accurate by the present author at the time the present series of studies began because of the basic similarities of habit and pollen type. The concept did not come into question until the pollen of the *Lepidaploa* com-

plex was subjected to detailed SEM study. The recognition of two groups based on pollen differences was followed by the discovery of style base and glandular trichome characters that are of generic importance. The present redistribution of the series *Flexuosae* of Jones is based on the characteristics discussed below under the headings pollen, inflorescences, involucre, nonglandular trichomes, style bases, and glands. The latter refer particularly to the glands of the anther appendage. The generic distinctions emphasized are those from the two larger members of the complex, *Lepidaploa* and *Lessingianthus*.

Pollen

As in all members of the *Lepidaploa* complex, the pollen of *Chrysolaena* has the exine organized into a lophate pattern. The actual pattern is one referred to by Stix (1960) in her major study of Asteraceous pollen as the *Vernonia cognata*-Type. The same type has more recently been designated by Jones (1979a) as type C. The type is distinguished by having a single areolae at each pole, no cross-walls in the colpus immediately above or below the pores, and usually two areolae equatorially across the intercolpar region. There are sometimes three areolae in one or two of the intercolpar regions of a grain (Fig. 1). The type C pattern is found in all the species that have been placed in the series *Flexuosae*, and all those recognized here as *Chrysolaena*.

Under detailed SEM examination, the pollen of series *Flexuosae* of Jones (1981) shows two types. The majority of the species shows the "rhizomatous" structure of the exine crests (Figs. 1-4) that is characteristic of the genus *Lepidaploa* and its close relatives *Stenocephalum* and *Echinocoryne* (Robinson 1987a, b). The remaining two species, examined by SEM and light microscopy, *V. simplex* and *V. desertorum*, show no such rhizomatous structure. The latter species are the same ones that Baker

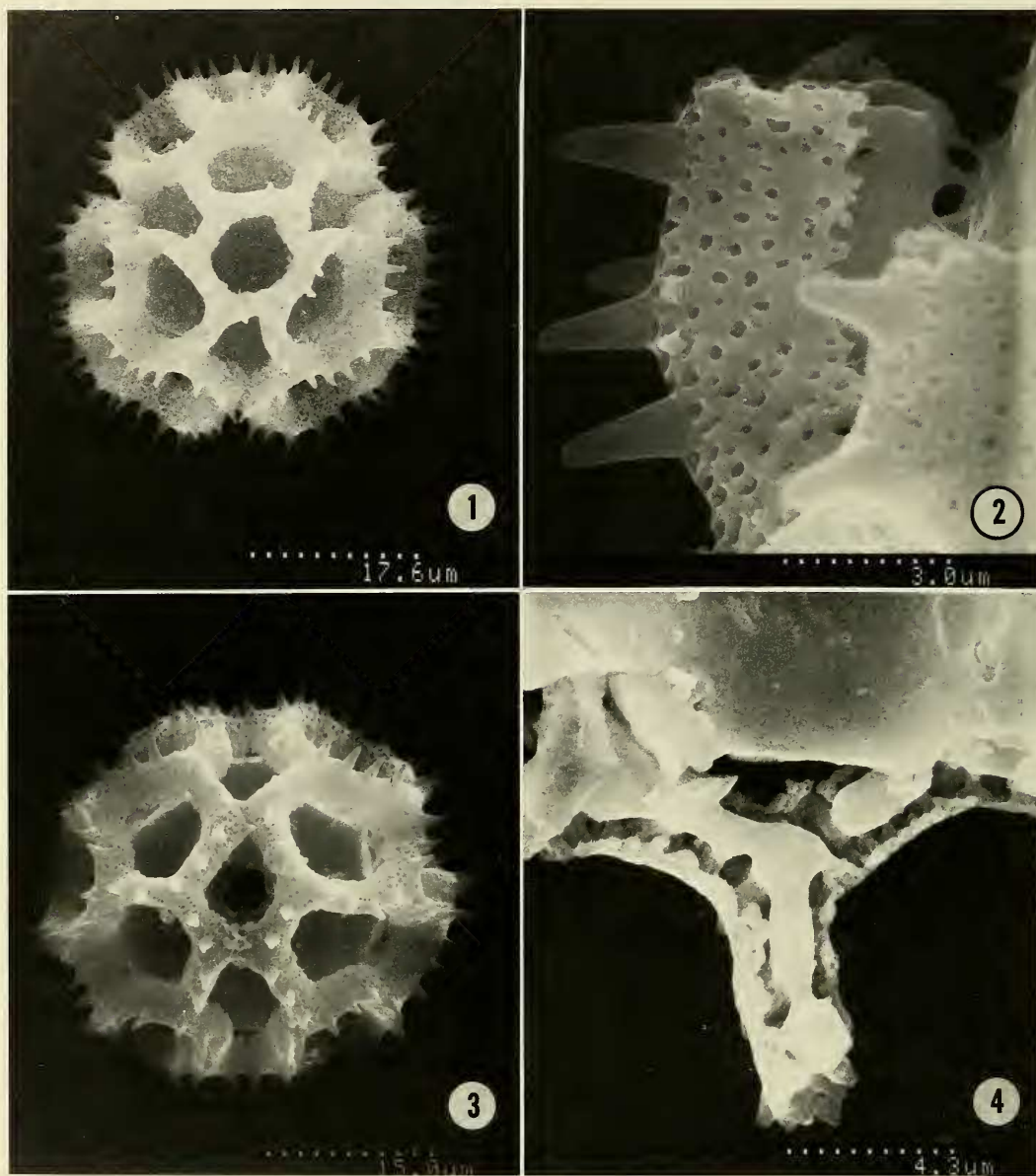
(1873) placed in his subsect. *Oligocephalae*, separate from his placement of those now included in *Chrysolaena*. These two species have pedunculate heads, which distinguishes them from others included in the *Flexuosae* by Jones. The characters by which the latter two species resemble *Chrysolaena* can be considered comparatively superficial. The non-rhizomatous pollen crests, the pedunculate condition of the heads, and the lack of glands on the achenes and anther appendages are all characters that distinguish the species from *Chrysolaena* and indicate their proper placement in *Lessingianthus* (Robinson 1988).

Inflorescences

The sessile condition of the heads in all the members of *Chrysolaena* that were recognized by Jones in his series *Flexuosae* correlate with the rhizomatous pollen crests in indicating a close relationship to the genus *Lepidaploa*. As in the latter genus, the inflorescences of *Chrysolaena* characteristically show a seriate-cymose condition where every head has a terminal position and the continuation of the apparent primary branch is through a lateral branch. Each head except the terminal one appears sessile as a result of the lateral branch being immediately below the head. The only member of *Chrysolaena* in which the character seems to fail is the species added to the group in this treatment, *Chrysocoma oligophylla*. Even in this species, displacement of the lateral branches from immediately below the heads seems rare. The pedunculate appearance seems to be mostly derived from the presence of many branches that usually have only one head. No other character indicates that the species should be excluded from the genus.

Involucre

The involucre of *Chrysolaena* have bracts of graduated lengths, but they show none of



Figs. 1-4. *Chrysolea herbacea* (Vell.) H. Robinson, pollen. 1. Polar view showing polar areola and variation between two and three intercolpar areolae at periphery. 2. Lateral view of crest showing weak basal attachment of rhizome. 3. Colpar view with colpus partially collapsed and appearing interrupted. 4. Crest stripped from surface showing underside with rhizome.

the additional differentiation in shape and texture seen in many species of *Lepidaploa*. The lack of differentiation is reminiscent of *Lessingianthus*, and it may be a retained

primitive condition, rather than a reduction.

The ratio of involucre bracts to flowers in the heads of *Chrysolea* is 1:1-2:1. The

comparative number of bracts is generally less than in either *Lepidaploa* or *Lessingianthus*, both of which tend to have 2:1–3:1 ratios. The shift in basic ratio is in the opposite direction from that seen in two other genera of the complex, *Stenocephalum* and *Echinocoryne*, where the involucre bracts occur in comparatively higher numbers.

Nonglandular Trichomes

The stems, leaves, and involucre bracts of *Chrysolaena* bear long sericeous or lanate hairs that contribute to the similarity in appearance of the plants. The hairs are yellowish to brownish and vary from straight to slightly flexuous. The hairs on the leaves vary from very dense in *V. herbacea* to sparse in *V. platensis*. Pubescence density in the inflorescence on the branches and involucre bracts is comparatively uniform in all the species. The hairs as seen in the species *V. herbacea* are the basis of the generic name *Chrysolaena*.

Style Bases

The presence or absence of nodular style bases is discussed in greater detail in treatments of the genera *Lessingianthus* (Robinson 1988) and *Lepidaploa* (Robinson in prep). The presence of a node seems basic to many neotropical members of the tribe Vernonieae and is regarded as basic to the *Lepidaploa* complex. However, three different genera of the complex appear to have lost the node. There is little or no node in *Stenocephalum* (Robinson 1987a), and *Lessingianthus* has essentially no node in its more than ninety species (Robinson 1988). *Chrysolaena* also lacks a distinct node. The only enlargements seen are the result of the basal row of sclerified cells holding their shape while the softer tissue above contracts. This condition contrasts strongly with the usually large and sometimes ornamented basal disk seen in *Lepidaploa*. Apparently, the three genera lacking basal stylar

nodes have separately lost this structure. No function is presently known for the structure in the tribe, and therefore no functional shift is known that could explain the three separate losses. The essential coincidence of the character with generic concepts is convenient for the taxonomist, but it does raise unresolved questions about the precise nature of the phyletic gaps between the genera.

Glands

Structures sometimes referred to as short-stalked capitate glands are a type of a biserial hair characteristic of the Asteraceae. They are notable in the family for the sesquiterpene lactones that they produce. They can be found on stems, leaves, involucres, corollas, anthers, style branches and achenes, but their appearance on vegetative parts, involucres, or corollas does not necessarily correlate with occurrence on anthers or achenes. In fact, only the tribes Heliantheae and Vernonieae commonly have glands on the anther appendages. *Chrysolaena* is one genus of the Vernonieae that seems to characteristically have glands on the anther appendages, but it is the only such genus in the *Lepidaploa* complex. In *Chrysolaena* the glands occur over most of the length of the appendage. They have been seen in all specimens of all but one species. The anther appendages of *V. herbacea* usually lack glands, although a few have been seen in some specimens.

The achenes of *Chrysolaena* also usually have glands among the setulae, at least near the base. Such glands do not occur in *Lessingianthus*, but they are found in various species of *Lepidaploa*. Glandular achenes and rhizomatous pollen crests both indicate a closer relationship of *Chrysolaena* to *Lepidaploa* than to *Lessingianthus*.

The various characters cited for *Chrysolaena* in some cases correlate with *Lepidaploa* and in others with *Lessingianthus*. The rhizomatous pollen crests are considered evidence that the relationship is closer

to *Lepidaploa*. The latter view is strengthened by the basically sessile condition of the heads and by the common occurrence of glands on the achene. The lack of a basal stylar node and the habitual resemblance to *Lessingianthus* subg. *Oligocephalus* seems to be the only basis for relating *Chrysolaena* to *Lessingianthus*, but these resemblances seem to be the result of independent reductions. *Chrysolaena* violates the generic limits of the two larger genera in a number of minor characters, such as the involucre/flower ratio and the pedunculate heads found rarely in one species. Still, one character, the glands on the anther appendages, is a unique departure from all other members of the *Lepidaploa* complex. Even though the glands are usually missing in one of the species, their presence is too consistent in the genus as a whole to be ignored. The combination of the glanduliferous appendages and the other discrepancies from *Lepidaploa* and *Lessingianthus* lead to the present recognition of *Chrysolaena* as a distinct genus.

The generic name is derived from the words *Chryso-* meaning golden and *laena* meaning cloak.

***Chrysolaena* H. Robinson, gen. nov.**

Vernonia subsect. *Flexuosae* Cabrera, Darwiniana 6:329. 1944. Type: *Vernonia flexuosa* Sims.

Vernonia series *Flexuosae* (Cabrera) Jones, Rhodora 81:442. 1979. Type: *Vernonia flexuosa* Sims.

Vernonia series *Verbascifoliae* Jones, Rhodora 81:438. 1979 as to type but not as to intent. Type: *Vernonia verbascifolia* Less.

Plantae herbaceae perennes ad 2.5–15.0 dm altae xylopodiales, caules folia et bracteae involucri flave vel fulve sericeae vel lanatae. Caules erecti interdum abbreviati sub inflorescentia non ramosi. Folia alterna vel basiales saepe superne descrenentia sessilia ovata vel linearia vel obovata supra et subtus parce vel dense sericeae vel lan-

atae, nervis secundariis ascendentiter pinnatis vel sublongitudinalibus. Inflorescentiae interdum scaposae distincte cymosae saepe seriate cymosae, ramis dense sericeis; capitula sessilia raro breviter pedunculata. Involucra leniter subimbricata subgraduata 1–2-plo quam floribus 3–5-seriata, bracteis lanceolatis acutis. Flores 10–65; corollae purpureae, lobis plerumque glanduliferis caetera glabris in nervis apice conjunctis et leniter incrassatis; appendices antherarum plerumque glanduliferae; basi stylosum non noduliferi. Achaenia dense setulifera et plerumque glandulifera plerumque 5-costata; carpopodia turbinata, cellulis oblongis in parietibus lateralibus porulosis; setae pappi interiores capillares elongatae apice non lateriores, squamae exteriores breviores. Grana pollinis in diametro 40–50 μm lophata ad polos uni-areolata intercolpe dupliciter areolata (typus C), cristis rhizomataceis.

Type. — *Vernonia flexuosa* Sims.

Chromosome numbers of $N = 17$ and $N = 34$ have been reported in members of *Chrysolaena* (Jones 1979b).

The genus is concentrated geographically in central and southern Brazil and northern Argentina, and extends westward into Bolivia with one occurrence in Peru. The genus contains the following seven species of which six have been recently treated by Jones (1981) as members of the *Vernonia* series *Flexuosae*.

***Chrysolaena flexuosa* (Sims)**

H. Robinson, comb. nov.

Vernonia flexuosa Sims, Bot. Mag. 51, pl. 2477. 1824. *Vernonia montevidensis* Nees ex Otto & Dietr., Allg. Gartenzeitung 1: 229. 1833. *Cacalia flexuosa* (Sims) Kuntze, Rev. Gen. Pl. 2:970. 1891. Argentina, Brazil (Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay, Uruguay.

***Chrysolaena herbacea* (Vell.)**

H. Robinson, comb. nov.

Chrysocoma herbacea Vell., Fl. Flum. 330. 1825. *Vernonia obovata* Less., Linnaea 4:

279. 1829. *Vernonia densevillosa* Mart. ex DC., Prodr. 5:43. 1836. *Vernonia chrysophylla* Gardn., Lond. J. Bot. 6:417. 1847. *Cacalia obovata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia paucifolia* Rusby, Mem. Torrey Bot. Club 3: 50. 1893. *Vernonia herbacea* (Vell.) Rusby, Mem. Torrey Bot. Club 4:209. 1895. Bolivia, Brazil (Amazonas, D.F., Goiás, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, São Paulo), Peru (Junin).

Chrysolaena lithospermifolia (Hieron.)
H. Robinson, comb. nov.

Vernonia lithospermifolia Hieron., Bot. Jahrb. Syst. 22:694. 1897. Brazil (Mato Grosso, Minas Gerais, Paraná, Santa Catarina, São Paulo), Paraguay.

Chrysolaena oligophylla (Vell.)
H. Robinson, comb. nov.

Chrysocoma oligophylla Vell., Fl. Flum. 324. 1825, Atlas 8: pl. 2. 1835. *Cacalia oligophylla* (Vell.) Kuntze, Rev. Gen. Pl. 2: 968. 1891. *Vernonia hypochlora* Malme, Kungl. Svensk Vetenskapsakad. Handl. 12(2):12. 1933. Brazil (Paraná, Santa Catarina, São Paulo). The identity of the Vellozo species is briefly discussed in the treatment of *Lessingianthus* (Robinson 1988). The species name has been incorrectly associated with the habitually very similar *V. cephalotes* DC.

Chrysolaena platensis (Spreng.)
H. Robinson, comb. nov.

Conyza platensis Spreng., Syst. Veg. 3:509. 1826. *Vernonia platensis* (Spreng.) Less., Linnaea 4:312. 1829. *Vernonia cognata* Less., Linnaea 6:670. 1831. *Vernonia senecionea* Mart. ex DC., Prodr. 5:54. 1836. *Cacalia cognata* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia platensis* (Spreng.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia sceptrum* Chod., Bull. Herb. Boissier, ser. 2, 2:303. 1902. Argentina, Brazil (Minas Gerais, Paraná, Rio

Grande do Sul, Santa Catarina, São Paulo), Paraguay, Uruguay.

Chrysolaena propinqua (Hieron.)
H. Robinson, comb. nov.

Vernonia propinqua Hieron., Bot. Jahrb. Syst. 22:695. 1897. *Vernonia lepidifera* Chod., Bull. Herb. Boissier, ser. 2, 2:304. 1902. Argentina (Misiones), Brazil (Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), Paraguay.

Chrysolaena verbascifolia (Less.)
H. Robinson, comb. nov.

Vernonia verbascifolia Less., Linnaea 4: 310. 1829. Argentina (Corrientes, Misiones), Brazil (Paraná), Paraguay.

Acknowledgments

The pollen specimens were prepared by Mary Sangrey using facilities of the Botany Department Palynological Laboratory. The photographs were prepared by Suzanne Braden of the Smithsonian Museum of Natural History SEM Laboratory using a Hitachi 570 scanning electron microscope.

Literature Cited

- Baker, J. G. 1873. Compositae I. Vernoniaceae. in C. F. P. Martius, Flora Brasiliensis 6(2):2-179.
Cabrera, A. L. 1944. Vernoniaceas Argentinas (Compositae).—Darwiniana 6:19-379.
Jones, S. B. 1979a. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernoniaceae) in the New World.—Rhodora 81:425-447.
———. 1979b. Chromosome numbers of Vernoniaceae (Compositae).—Bulletin of the Torrey Botanical Club 106:79-84.
———. 1981. Revision of *Vernonia* series *Flexuosae* (Compositae: Vernoniaceae). Brittonia 33:214-224.
Robinson, H. 1987a. Studies in the *Lepidaploa* complex (Vernoniaceae: Asteraceae). I. The genus *Stenocephalum* Sch. Bip.—Proceedings of the Biological Society of Washington 100:578-583.
———. 1987b. Studies in the *Lepidaploa* complex (Vernoniaceae: Asteraceae). II. A new genus, *Echinocoryne*.—Proceedings of the Biological Society of Washington 100:584-589.

- . 1987c. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). III. Two new genera, *Cyrtocymura* and *Eirmocephala*.—Proceedings of the Biological Society of Washington 100: 844–855.
- . 1988. Studies in the *Lepidaploa* complex (Vernonieae: Asteraceae). IV. The new genus *Lessingianthus*.—Proceedings of the Biological Society of Washington 101:929–951.
- Stix, A. 1960. Pollenmorphologische Untersuchungen an Compositen. *Grana Palynologica* 2:41–104.

Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.